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THE EVOLUTION AND BIOGEOGRAPHY OF THE MYGALOMORPH SPIDER FAMILY HEXATHELIDAE (ARANEAE, CHELICERATA)

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ABSTRACT

The family Hexathelidae is newly erected. Three subfamilies are recognized: Plesiothelinae, for the monotypic Tasmanian genus *Plesiothele*; Macrothelinae, confined to *Macrothele*, *Porrhothele* and *Atrax*; and the Hexathelinae include *Hexathelidae*, *Scotinoecus*, *Bymainiella*, *Paraembolides*, gen. nov. and *Terania*, gen. nov. The synapomorphic character required for group membership is numerous labial cuspules. Using the size of the anterior lateral spinnerets, the development of megaspines on the first tibia of males, the paraembolic apophysis, and shape of the labium and other characters, the evolution of subfamilies, genera and some species is discussed using Hennigian principles. A biogeographic hypothesis is proposed using the vicariance events of Plate Tectonic theory. The sister group of the Hexathelidae is the Dipluridae, and the sister group of both is the Mecicobothriidae. The subfamily Ischnothelinae is erected to receive those genera of the traditional Macrothelinae that have no labial cuspules.

INTRODUCTION

The Mygalomorphae are an important group of spiders that have been neglected in discussions of evolution and biogeography. They are important as they possess features widely regarded as plesiomorphic in spiders, and they give a major perspective to evolutionary hypotheses. Pocock (1903) is the only arachnologist of wide knowledge to propose a theory to explain the contemporary distribution of mygalomorphs. Unfortunately, Pocock did not depart from the widely held views of faunal origins of his time, whose protagonists maintained that southern migrations of northern species occurred across land bridges, presumed to have been static for some time.

Evolutionary hypotheses are lacking, and even now an acceptable phylogeny of the Mygalomorphae does not exist. Classificatory keys required ease of application, and monothetic groups, which were usually made up of paraphyletic taxa sharing only plesiomorphic characters, resulted. With Hennig (1966) began the widespread acceptance of phylogenetic systematics, in which a shared derived character is needed to join two sister groups. This allowed the formulation of empirically testable hypotheses.

The weakness of the cladistic (= phylogenetic sensu Henning) methodology lies in the decision about the direction of character change, upon which Brundin (1966) remarked, may be completely right or wrong - there being no alternative. This apparent weakness of cladistic methodology becomes its strength, as further characters may then be used to test the polarity of characters originally used, and so test the overall cladogram.

Within the Dipluridae, the Hexathelinae are historically regarded as primitive spiders and are diagnosed by primitive characters. However, their patristic similarity to one another suggests monophyly and the Mesothelae (= Liphistiomorphae, see Platnick and Gertsch 1976) attest the possibility of plesiomorphic taxa being monophyletic. Raven (1978) re-examined the sub-family Hexathelinae taxonomically, and arrived at conservative conclusions about the ranks of certain taxa. At that time the theory proposed herein was in its genesis, and the conclusions about the phylogenetic relationships of the genera involved were tempered.

In this study, I shall present evidence which strongly suggests that, at least in the Hexathelinae, the paraembolic apophysis - the probable homologue of the conductor, is present only in more derived genera, and is thereby apomorphic.

Considerable attention has been recently directed to the phylogenetic position of the Liphistiidae, and in cladistic analyses, Platnick and Gertsch (1976) and Kraus (1978) have used the unique sexual morphology of *Liphistius* and related genera to support their theory. The male liphistiid palpal bulb appears to be a surprisingly complex structure for a generally plesiomorphic group of spiders. Consequently, the traditional interpretation of this enigmatic complexity has generally been that complexity infers apomorphy. Gertsch (in Platnick and Gertsch 1976) and Kraus (1978) present the alternative hypothesis that, in fact, the liphistiid palp is plesiomorphic, and that less complex palpal bulbs have been the result of multiple parallel reductions of structures - not necessarily an equivalent process to simplification. The basis of this hypothesis is the correlation of the bipartite male palpal bulb with the bipartite nature of the corresponding female genitalia, and distribution of the bipartite condition in the atypids and hypochiloids as well as liphistiids.

SYSTEMATICS

Family Hexathelidae (Simon, 1892)

Diagnosis.—Mygalomorph spiders with eight eyes and a transverse fovea; carapace lacking hairs. One or two rows of teeth on the cheliceral furrow; no rastellum. Maxillae longer than wide; ectal anterior corner with slight angular production and with serrula; armed with numerous cuspules. Labium square to wide; armed with numerous cuspules. Sternum separated from labium by sigmoid groove; six sigilla. No leg scopula in females. Three claws; one row of teeth on superior claws; inferior claw well developed. Trichobothria in two rows on tibiae, one row on metatarsi, and one irregular to straight row on tarsi. Trichobothrial bases collariform. Four to six spinnerets; apical segment of posterior laterals digitiform.

Male palp simple or with paraembolic apophysis; anterior tibiae of males modified. Internal genitalia of females with one or rarely two lobes on each side - the lobes uni- or multilocular.

Remarks.—The elevation of this family is based upon the synapomorphous possession of numerous labial cuspules by all of its members. The family is divided into 3 sub-

families: Hexathelinae, Macrothelinae and Plesiothelinae.

The sister group of the Hexathelidae.—The sister group of the Hexathelidae is the Dipluridae, and together these two families form the sister group of the Mecicobothriidae. This is based upon the absence of abdominal tergites in the former families. These three families may be united in the presence of a maxillary serrula in most genera (see Platnick 1977). In the Dipluridae, labial cuspules are rarely present, and when present are very few; and all diplurid genera so far examined have corrugiform trichobothrial bases. All hexathelid genera have collariform bases. Although the corrugiform condition may not be a synapomorphy for the diplurids, it is another difference from the Hexathelidae.

Subfamily Hexathelinae (Simon, 1892)

Diagnosis.—Six spinnerets. True megaspines present on first tibiae of males. Caput of females low.

Checklist of genera.—*Hexathele* Ausserer, 1871; *Scotinoecus* Simon, 1888; *Bymainiella* Raven, 1978; *Terania*, gen. nov.; *Paraembolides*, gen. nov.

Remarks.—The genera constituting this subfamily are unchanged from Raven (1978), except that *Plesiothel* is removed, and *Bymainiella* is now divided into three genera. The reasons for these changes will be made clear below. A 'megaspine' is a thickened spine which crowns an apophysis; it replaces the term 'spur' which is misleading (Raven, 1980).

The diagnoses of *Hexathele* and *Scotinoecus* are those given previously (Raven 1978), except that *Scotinoecus* may have as few as 10 labial cuspules (pers. obs.).

Bymainiella Raven

Bymainiella Raven 1978: p. 56. Type-species by subsequent designation: *Hexathele terraereginae* Raven, 1976.

Diagnosis.—Males with a prominent distal megaspine on tibia I, interfacing with a prolateral metatarsal flange. Male palpal bulb pyriform or with a broad protuberance. Female internal genitalia with one bifurcate lobe on each side. Tarsal trichobothria in a single line. Labium wider than long. Up to thirty cuspules on labium. No spines on leg tarsi.

Checklist of species.—*Hexathele terraereginae* Raven, 1976 (type-species); *Bymainiella lugubris* Raven, 1978; *Bymainiella polesoni* Raven, 1978; *Bymainiella monteithi* Raven, 1978.

Remarks.—This is the *Bymainiella terraereginae* species-group of Raven (1978).

Terania, gen. nov.

Diagnosis.—Males with a single distal megaspine on a raised apophysis on tibia I; metatarsus I proximally excavate, without a flange; palpal bulb pyriform. Labium almost as long as wide or wider. Spines usually present on all tarsi. Tarsal trichobothria in a single line. Up to thirty cuspules on labium.

Type-species.—*Hexathele montana* Hickman 1927

Etymology.—*Terania* is a euphonious combination of letters which conveys the earth; the gender is feminine.

Remarks.—Apart from the type-species, this genus includes only *Bymainiella otwayensis*. *Paraembolides tubrabucca* shares only plesiomorphic characters with the species of *Terania*, and is removed to *Paraembolides*.

Paraembolides, gen nov.

Diagnosis.—Males with a single distal megaspine, but not on a raised apophysis, on tibia I, no metatarsal flange; palpal bulb with paraembolic apophysis. Labium much wider than long. Spines absent from anterior tarsi. Tarsal trichobothria in a single line. Up to thirty cuspules on labium.

Checklist of species.—*Bymainiella boycei* Raven, 1978 (type-species); *Bymainiella boydi* Raven, 1978; *Bymainiella brindabella* Raven, 1978; *Bymainiella cannoni* Raven, 1978; *Bymainiella grayi* Raven, 1978; *Bymainiella montisbossi* Raven, 1978; *Bymainiella tubrabucca* Raven, 1978; *Bymainiella variabilis* Raven, 1978.

Etymology.—This name is derived from the paraembolic apophysis which characterizes the group; the gender is feminine.

Remarks.—Although *Paraembolides tubrabucca* was originally regarded as a sister species of *Terania montana*, the presence of a small paraembolic process on the former indicates affinities with species placed in *Paraembolides*.

Subfamily Macrothelinae (Simon, 1892)

Diagnosis.—Four spinnerets. Labium almost as wide as long or longer. Cuspules on labium typically very numerous. True megaspines absent on tibia I, tibia I densely spined and incrassate; may have mid-ventral apophysis on tibia II.

Checklist of genera.—*Macrothele* Ausserer, 1871; *Porrhothele* Simon, 1892; *Atrax* Pickard-Cambridge, 1877.

Remarks.—Prior to this study the Macrothelinae included *Allothele*, *Cethegus*, *Evagrella*, *Evagrus*, *Holothele*, *Ischnothele*, *Lathrothele*, *Linothele*, *Phyxioschaema* and *Thelechoris*, as well as those listed above. The type-species of *Holothele* and *Linothele* have been examined. *Holothele* is a theraphosid, and probably is a synonym of *Stichoplastus*, and *Linothele* is a junior synonym of *Diplura*.

The sub-family Macrothelinae is limited to those genera with cuspules on the labium as well as on the maxillae. However, such genera also have digitiform posterior lateral spinnerets, a raised caput, and usually have few hairs on the carapace. This is in contrast to the *Evagrus*-like genera which have long posterior lateral spinnerets, a low caput, and a hirsute carapace. The redefinition of the Macrothelinae leaves those diplurids with four spinnerets and one row of teeth on the superior claws without a subfamily group name. I propose *Ischnothele* as the nominate genus, as Pickard-Cambridge (1897) had previously suggested.

Macrothele Ausserer

Macrothele Ausserer 1871: 181. Type-species by original designation: *Mygale calpeiana* Walckenaer 1805.

Diagnosis.—Posterior sternal sigilla much larger than anterior pairs. A row of teeth on cheliceral promargin only or with an additional row of smaller teeth on retromargin. Tibia I of males incrassate. Spines present on tarsi.

Remarks.—Some *Macrothele* species have a reduced number of labial cuspules whereas most species of this and other macrothelini genera have numerous cuspules. The species constituting this genus have not been critically examined and are as listed by Bonnet (1959) except that *M. aculeata* is excluded because it is a ctenizid (Main, pers. comm.).

Porrhothele Simon

Porrhothele Simon 1892: 182. Type-species by original designation and monotypy: *Mygale antipodiana* Walck. 1837.

Diagnosis.—Posterior sternal sigilla small, marginal. A row of teeth only on cheliceral promargin. First tibia of males incrassate. No spines on leg tarsi.

Remarks.—Forster and Wilton (1968) give an excellent revision of this genus, consequently no extensive diagnosis is necessary. *Porrhothele* is very similar to *Macrothele* in sexual morphology; however, they may be readily distinguished in that *Porrhothele* has no spines on the leg tarsi.

Atrax Pickard-Cambridge

Hadronyche Koch 1873: 463. Type-species by original designation and monotypy: *H. cerberea* Koch 1873.

Atrax Pickard-Cambridge, O. 1877: 26. Type-species by original designation and monotypy: *A. robustus* Pickard-Cambridge 1877.

Styphlopis Rainbow 1913: 6. Type-species by original designation and monotypy: *S. insularis* Rainbow 1913.

Euctimena Rainbow 1914: 249. Type-species by original designation and monotypy: *E. tibialis* Rainbow 1914.

Pseudoatrax Rainbow 1914: 261. Type-species by original designation and monotypy: *P. moreau* Rainbow 1914.

Poikilomorpha Rainbow 1914: 265. Type-species by original designation and monotypy: *P. montana* Rainbow 1914.

Anepsiada Rainbow and Pulleine 1918: 167. Type-species by original designation and monotypy: *A. ventricosa* Rainbow and Pulleine 1918.

Diagnosis.—Posterior sternal sigilla large. A row of teeth on both cheliceral margins. First tibia of males not incrassate.

Remarks.—*Hadronyche* is the senior subjective synonym of the medically infamous *Atrax*. However, a submission is believed to be before the International Commission for Zoological Nomenclature for the suppression of *Hadronyche*; the genus is also currently being revised (M. Gray, in litt.).

Atrax is probably the most contentious genus of this family. However, on the basis of its derived characters it is not closely related to any other group in the Dipluridae. Moreover, its affinities with other genera of similar facies, such as the atypoid genera, must be discounted as the maxillae are not sufficiently modified to allow it to be a member of that group. Other characters that are discussed below, such as the presence of a maxillary serrula, indicate that *Atrax* is more closely related to the Hexathelidae and Dipluridae.

Subfamily Plesiothelinae, new sub-family

Diagnosis:—Six spinnerets. Terminal segment of anterior lateral spinnerets enlarged, and apical segment domed. First tibia of male without modifications; metatarsus I bent; palpal bulb pyriform, with a short twisted embolus.

Remarks:—This subfamily has, as its only member, the monotypic genus, *Plesiothel* Raven 1978.

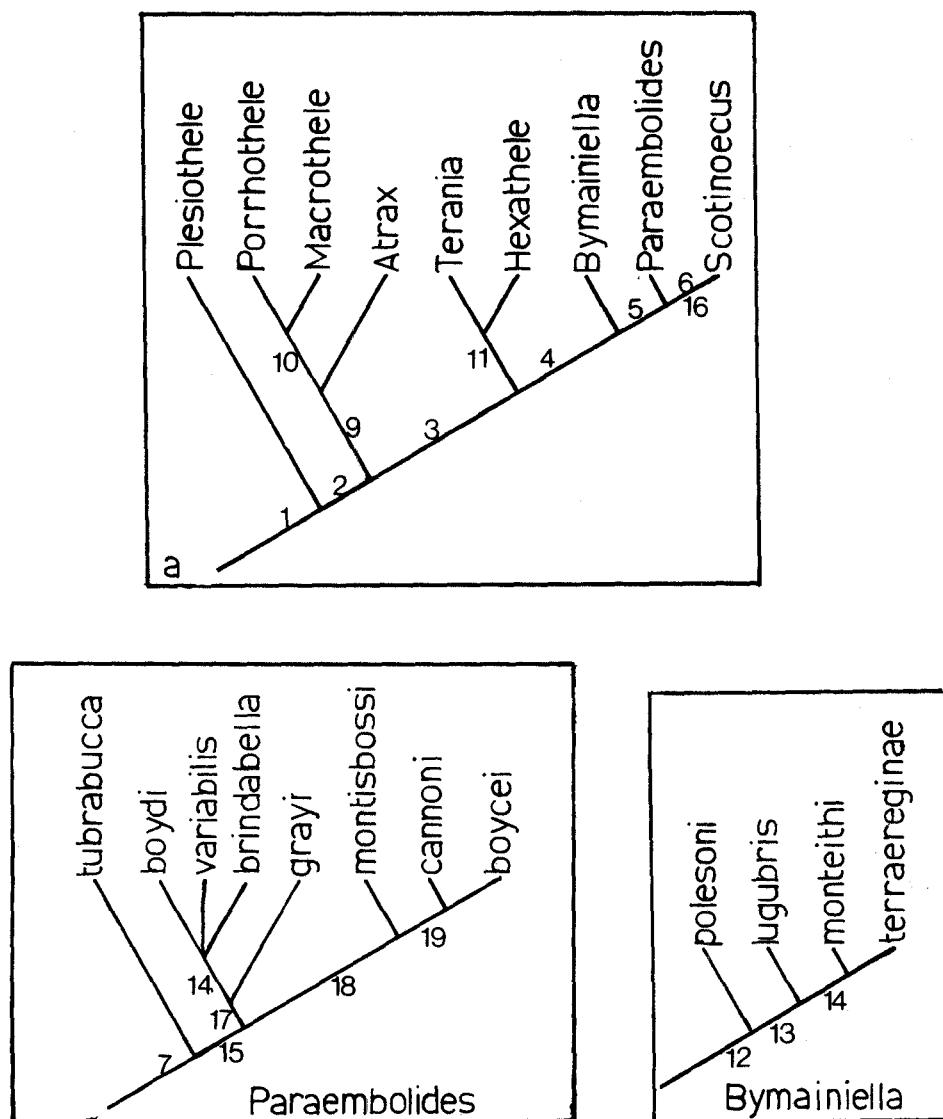


Fig. 1.—Cladograms of the family Hexathelidae. Table 1 shows characters associated with numbers.

THE CONSTRUCTION OF THE CLADOGRAM

The members of each subfamily and genus are taken from the cladogram (Fig. 1a) of the family. The construction of the cladogram, in following the principles of phylogenetic systematics expounded by Hennig (1966) and Brundin (1966), requires that each group must have derived characters (Table 1) uniquely shared by the members of that group. In the cladogram, immediately below the fusion point of two sister groups, is the number of the character that is regarded as the synapomorphy of the taxa above that point. The term 'ancestor', as used here, refers to a hypothetical taxon not an individual.

Characters

1. The maxillary and labial cuspules.—In the Mygalomorphae the presence of numerous cuspules on the maxillae is unique, and thus it may be this character, which although polythetic, is the autapomorphy of the Mygalomorphae. As confirmation of this, cuspules do not occur in the Mesothelae, thus their presence in the Mygalomorphae may, by outgroup comparison, be regarded as apomorphic. This does not invalidate the reverse polarity indicated by Platnick and Shadab (1976) for the Actinopodidae, because that is in a widely separated clade, in which the loss of cuspules may be secondary.

The dense (= closely grouped) spination of the labium is, on the other hand, an unusual character. Numerous labial cuspules are present in migids, barychelids and theraphosids, but these clades are widely separated from the group under study. Within the three-clawed Mygalomorphae, only the Hexathelidae and the ctenizid genera, *Bessia* and *Spiroctenus*, have numerous labial cuspules. Thus, within the Dipluridae (s. lat.) and Mecicobothriidae, regarded as sister groups by Platnick (1977) in the joint possession of a maxillary serrula, the Hexathelidae is the only group that has numerous cuspules on the labium. It is upon this basis that the Hexathelidae is regarded as a monophyletic group.

2. The male palpal embolus.—In the Mygalomorphae, the embolus is commonly elongate to whip-like; in the Mesothelae, the embolus is short; whereas in the Araneomorphae, the apomorphic sister group of the Mygalomorphae, the embolus is most widely elongate or whip-like. Thus, by out-group comparison and abundance, the short embolus is regarded as a plesiomorphic retention, and the elongate embolus derived. An important aspect of this character is that, although it is clearly apomorphic, its widespread presence in the Mygalomorphae strongly indicates that it may have independently evolved to the same condition many times.

3. The modification of the first leg of the male.—The megaspines which occur on one or both pairs of anterior legs in male mygalomorphs, also occur in some araneomorphs, but are unusual in their function of maintaining the fangs of the female open during mating. Such megaspines do not occur in the more plesiomorphic Mesothelae, and are therefore considered apomorphic. Furthermore, the leg spination of immature males is identical to that of conspecific females, and it is only in the final moult of the male that spine dimorphisms and megaspines, if present, appear. Thus, the spination of females is believed to be more plesiomorphic than that of males.

The usual spination of the first tibia of female hexathelids is two ventral subdistal pairs followed apically by four spines set along the ventral tibial edge. A similar condition occurs in *Plesiothele*, and is regarded as plesiomorphic. As remaining taxa of the Hexathelidae have at least a group of numerous spines on the first tibia of males, this state is

Table 1.—Characters used in cladograms.

Plesiomorphic state	Apomorphic state
1. No labial cuspules	Numerous labial cuspules
2. Short embolus	Long embolus
3. Male tibia I without megaspines	Male tibia I with megaspines
4. Labium about as long as wide	Labium wider than long
5. Paraembolic apophysis absent	Paraembolic apophysis present
6. Anterior lateral spinnerets equal length to posterior medians	Anterior laterals clearly shorter than posterior medians
7. Spines present on anterior tarsi	Spines absent on anterior tarsi
8. Metatarsus I of males straight	Metatarsus I of males angular
9. Six spinnerets	Four spinnerets
10. Tibia I of males cylindrical	Tibia I of males incrassate
11. Metatarsus I of males cylindrical	Metatarsus I of males excavate
12. No flange on male metatarsus I	Flange present on male metatarsus I
13. ♀ patella III less than tibia III	♀ patella III greater than or equal to tibia III
14. 6-12 spines on ♀ metatarsus III & IV	4 spines on ♀ metatarsus III & IV
15. Paraembolic apophysis short	Paraembolic apophysis well-developed
16. Paraembolic apophysis thorn-like	Paraembolic apophysis spiniform
17. No hairs behind foveal bristles	Hairs present behind foveal bristles
18. No bristles lateral of eyes	Numerous bristles lateral of eyes
19. Paraembolic apophysis coniform	Paraembolic apophysis acute

considered an apomorphy that is correlated with the suggested apomorphy of the elongate embolus.

The character specifically involved here is 'true' (i.e. immovable) megaspines, and is probably the polythetic synapomorphy of the Hexathelinae, since all members have true megaspines and not simply a tibial apophysis thickly clad with spines, as in *Atrax formidabilis*.

4. The relative dimensions of the labium.—In the relatively plesiomorphic taxa to *Hexathele* on the cladogram, the width of the labium approaches its length, whereas in the more derived taxa the labium is considerably wider than long. Thus, in being confined to apomorphic taxa, a wide labium is regarded as apomorphic. The liphistiid labium is wide, and the araneomorph labium is highly variable.

5. The paraembolic apophysis.—This character requires some introduction as this term, that applies to an angular process arising adjacent to the embolic origin, was recently introduced by Raven (1978). In the male of *Scotinoecus fasciatus*, it was regarded as a 'conductor' by Schiapelli and Gerschmann de Pikelin (1968). It also occurs as a clearly supportive apophysis in some *Masteria* where, as a unilaterally grooved process, it distally supports the embolus (see Raven 1979); in some barychelid genera, it is present in a nominal state. In view of its widely dispersed presence in the Mygalomorphae, the paraembolic apophysis may be a plesiomorphic retention, or the result of parallel derivation in diverse clades; however, in the Hexathelinae it is apomorphic.

In the Atypidae, Antrodiaetidae and Mecicobothriidae, the embolus is usually entirely enclosed in a chitinous sheath, regarded as a conductor. It is here proposed that the paraembolic apophysis is the analogue of the conductor.

The Gertschian Theory: Gertsch (in Platnick and Gertsch 1976) has proposed that the bipartite palp of the Atypoidea and the palp of the Liphistiidae are plesiomorphic. This conclusion is based upon the correlation of the male palp with female characters. Thus, in contrast to the hypothesis proposed here, the parembolic apophysis would be interpreted as a more apomorphic reduction from the atypoid conductor. Also, the unencumbered palpal bulb so widespread in the Mygalomorphae, would be regarded as the most apomorphic state.

Gertsch states that: 'Two receptacles on each side is the standard number for the liphistiids, the three other atypoid families, the most generalized of the diplurids (*Scotinoecus* and *Hexathele*), and the primitive araneomorph spiders, the Hypochilidae and related families. . . . thus, in *Hexathele*, the paired receptacles persist on each side even though a single embolus is now present.'

Kraus (1978) uses the '2 + 2' terminology for the type of internal genitalia widespread in the Mygalomorphae and for the type in *Hypochilus* in which the two receptacula on each side join before discharging into a common atrium (through fusion?). Although Gertsch (in Platnick and Gertsch 1976) also used this '2 + 2' terminology, he restricts it to the typical configuration seen in *Atypus* and the Antrodiaetidae in which each of the four or more receptacula (2-11 on each side, Kraus 1978) discharge separately into the atrium.

Schiapelli and Gerschman de Pikelin (1962) have shown that the female *Liphistius* has complex internal genitalia, and hardly homologous with those of the Antrodiaetidae (see Coyle 1968, 1971, 1975). Moreover, of the two species of *Scotinoecus*, one has two separate receptacles on each side, and the second species has only one bifurcate receptacle on each side. In other hexathelids and the Dipluridae, no genus is known to have two receptacles on each side - all have one. Some *Masteria* have two lobes on each side although these are joined as part of a united receptacle leading to a single atrium (Raven 1979). Thus, although these two characters, the bipartite palp and the two pairs of

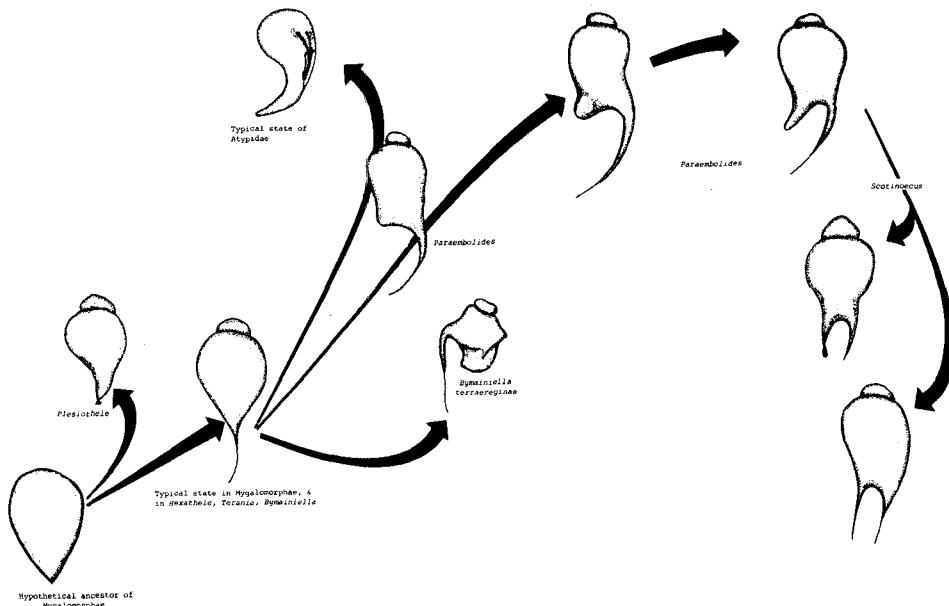


Fig. 2.—Evolution of the male palpal bulb in the Hexathelidae.

receptacles in the female, are correlated, neither can unequivocably indicate a direction of change and a third character must be introduced. This is the anterior lateral spinnerets.

6. The reduction of the anterior lateral spinnerets.—Within the Macrothelinae and Hexathelinae, the anterior lateral spinnerets exhibit a clearly reducing trend. In the Australian and New Zealand genera, the anterior lateral spinnerets are two-segmented, but are as large as, or larger than, the posterior median spinnerets; whereas in *Scotinoecus*, the anterior lateral spinnerets are strongly atrophied, especially in *S. cinereopilosus*. Ontogenetically, and by out-group comparison, the evolutionary trend of the anterior lateral spinnerets is toward absence. Finally, the result is the widespread four-spinnereted state. Thus, the atrophied anterior laterals are the most apomorphic state of the spinnerets seen in the Hexathelinae. In the Macrothelinae, the anterior lateral spinnerets are completely lost.

Correlated with the reduction in size of the anterior lateral spinnerets in the Hexathelinae, is the corresponding increase in the length of the paraembolic apophysis. In *Paraembolides*, the paraembolic apophysis varies from a low apophysis to a very acute process; in *Scotinoecus*, the paraembolic apophysis is maximally elongate. This strongly suggests that the development of the paraembolic apophysis is apomorphous within the Hexathelinae.

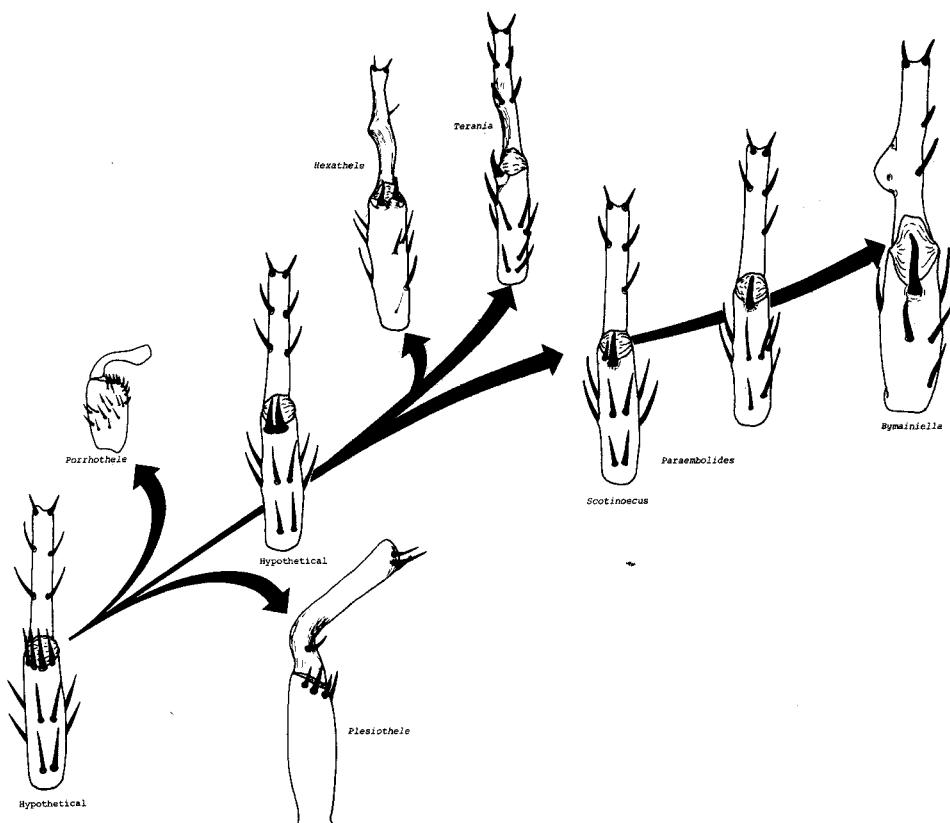


Fig. 3.—Evolution of the first tibia and metatarsus of males in the family Hexathelidae.

7. **Anterior tarsal spines.**—Anterior tarsal spines are functional in spiders which burrow, and are present in many mygalomorphs and in the Mesothelae. As both *Paraembolides* and *Scotinoecus* no longer excavate burrows, but occupy existing excavations, the presence of anterior tarsal spines is believed to be a plesiomorphic retention in *Scotinoecus*, and their absence in *Paraembolides* is the synapomorphy. The loss of tarsal spines is regarded as a parallelism, having occurred independently in *Bymainiella* and *Paraembolides*.

At this stage, the synapomorphies of all main stem groups have been discussed; the discussion of the synapomorphic characters of lateral clades follow.

8. **The first metatarsus of the male.**—In *Plesiothele*, the first metatarsus of the male is bent or sinuous, and uniform in diameter throughout its length. Because this condition is unique to *Plesiothele*, and as further shown by out-group comparison with male Mesothelae in which the metatarsi are straight and unmodified, it is regarded as apomorphic.

9. **Four spinnerets.**—All other hexathelinids have six spinnerets, thus the four spinnereted state of the Macrothelinae is apomorphic. The argument involved here is a logical extension of that given in 6.

10. **The first tibia of the male.**—In *Porrhothele* and *Macrothele*, the first tibiae of males are incrassate and densely covered with spines. This is unique within the family, and is thereby regarded as apomorphic. The autapomorphies of *Atrax*, *Macrothele* and *Porrhothele* are: strong teeth on both margins of the cheliceral furrow; moderately sized teeth on the retromargin of the cheliceral furrow; and the absence of tarsal spines respectively.

11. **The proximal excavation of metatarsus I of the male.**—The synapomorphy of *Hexathele* and *Terania* is the proximal excavation of the first metatarsus of males, which is maximally expressed in *Hexathele*. This should not be confused with the proximal metatarsal flange which occurs in *Bymainiella*, in which no reduction of the proximal diameter of the metatarsus is present.

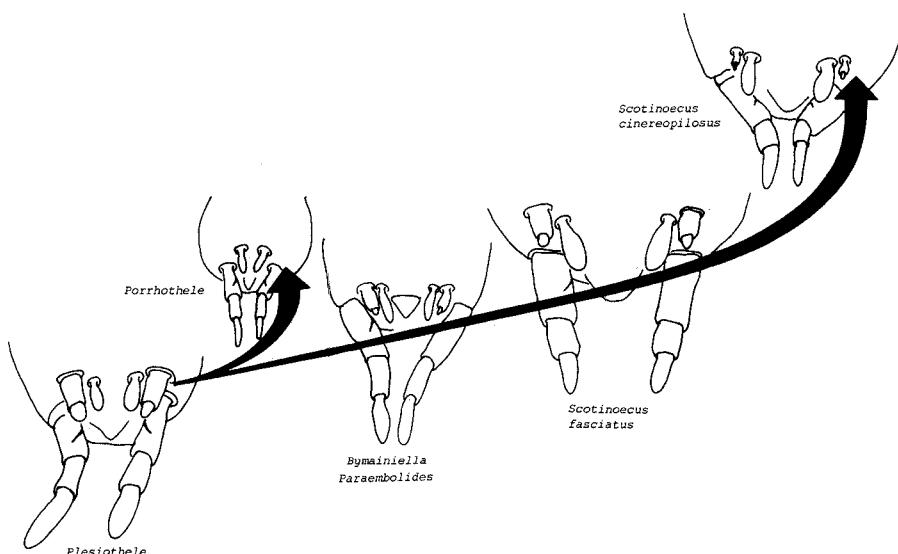


Fig. 4.—Evolution of the anterior lateral spinnerets in the family Hexathelidae.

12. The proximal metatarsal protuberance in the male.—Only in *Bymainiella* do males possess a conspicuous flange on the first metatarsus, and associated with this is the large sinuous tibial spur; because of their uniqueness these characters are regarded as apomorphic.

13. The equality of patella and tibia of females.—Throughout the Hexathelidae, females have a longer tibia than patella of the anterior legs, but in *Bymainiella lugubris*, *B. monteithi* and *B. terraereginae* the patella and the tibia are at least subequal; this is taken to be the apomorphic character which defines this species group. It should be noted here, that in burrowing mygalomorphs it is not unusual to find that the third patella is longer than the tibia. However, in these three *Bymainiella* species which exhibit this condition the two anterior pairs of legs also share this state.

14. Spination of the posterior metatarsi of females.—Four spines, dorsally and laterally on the posterior metatarsi, are more ordered than the more numerous and disordered state seen widely in the group, and it is this ordered condition which is regarded as the apomorphic state. The plesiomorphic state is from 6-12 spines on the metatarsi, and with different counts on each side of the spider.

15. The autapomorphies of *Scotinoecus*.—Two characters indicate the derived nature of this genus: the elongate nature of the paraembolic apophysis, and reduction of the anterior lateral spinnerets.

16. The paraembolic apophysis.—The paraembolic apophysis, as a vestigial mound or as an acute apophysis, occurs in both *Paraembolides* and *Scotinoecus*; it is most prominently developed in the latter, and in *Paraembolides tubrabucca*, occurs in the most plesiomorphic state - as a low triangular bump. Any states more highly developed than that of *P. tubrabucca* are regarded as more apomorphic, by an extension of argument 5.

A Synthesis

The Hexathelidae appear to be a monophyletic group which are characterised by the synapomorphous presence of numerous labial cuspules. Because some genera have retained anterior lateral spinnerets, they have been long regarded as the most plesiomorphic diplurids.

The short embolus and large anterior lateral spinnerets retained by *Plesiothele* place it basally in the phylogeny, prior to the development of true megaspines on male tibiae. With the loss of the anterior lateral spinnerets arose the ancestor of the Macrothelinae, now confined to *Atrax*, *Macrothele*, and *Porrhothele*. In the sister group of the Macrothelinae, the male ancestor of the Hexathelinae had already lost the two most lateral ventral spines on the tibiae, and the median pair of spines were undergoing an associated thickening. This male ancestor had two megaspines on the first tibiae and an unmodified metatarsus. From this male arose two groups. The apomorphic sister group consisted of *Bymainiella*, *Paraembolides* and *Scotinoecus*, in whose ancestor the labium was already wider than long and continued to widen. The plesiomorphic sister group consisted of *Hexathele* and *Terania*. The male ancestor of this group developed a proximally excavated first metatarsus, and retained a square labium.

The male ancestor of *Paraembolides* and *Scotinoecus* developed a paraembolic apophysis on the palpal bulb, and in the plesiomorphic ancestral sister genus, *Bymainiella*, males developed a proximal metatarsal flange on the first leg. In the 'Hexathele' clade, *Terania* lost one of the megaspines; the associated apomorphies in *Hexathele* were the distally alternating rows of trichobothria and the deeply excavate metatarsus of the male.

HISTORICAL BIOGEOGRAPHY OF THE HEXATHELIDAE

Spiders have often been regarded as poor subjects for biogeographic studies, and this is directly attributable to their well known high vagility. The rule for smaller and more readily dispersing spiders is indiscriminately considered the rule for all. However, the more cryptozoic or positively geotropic forms must be regarded as migrants. Thus, prominent past araneologists have maintained that many groups, such as the Mygalomorphae, owe their present distribution solely to their terrestrial dispersal (Pocock 1903), and presumably to transoceanic journeys on log rafts.

Platnick (1976) has indicated some of the practical objections to aerial dispersal and transoceanic colonization. Briefly, the problems are the prolonged dessicating atmosphere, coupled with the non-availability of water, and the astronomically remote chances of a juvenile successfully colonizing a suitable habitat, with low competition for resources, until mating had occurred with another such matured specimen. Although very small, the possibility of mygalomorphs colonising by log rafting cannot be dismissed. Indeed a gravid female of an arboreal mygalomorph species could survive a raft voyage, if the entire log or tree, in which the spiders burrow was already made, was dislodged, and became water-borne. But the dispersal hypothesis is not testable and is therefore not scientific (Platnick 1976, Platnick and Nelson 1978).

Further evidence suggesting that the mygalomorphs do not raft is their absence from the Sandwich Islands, Hawaii (Simon 1904) and indeed, most other oceanic islands. There are at least five notable exceptions to this. The diplurid genus, *Cethagus*, occurs in Australia and New Caledonia, although it does not occur in New Zealand (Main, in press). *Masteria*, another diplurid, and *Idioctis*, a barychelid, are known from the Samoan Islands; *Masteria* is also known from northern Australia, New Guinea, the Phillipines, Venezuela, the Caribbean islands and Chile (Raven 1979). *Migas* is known from Australia, New Zealand and New Caledonia. Zapfe (1961) describes *Migas* from South America but, from the description, it cannot be *Migas*. *Encyocrypta* occurs on New Caledonia and in Australia. In these cases, New Caledonia and the Samoan Islands are not true oceanic islands as they were once part of an Australian plate, which separated in the Cretaceous, and was uplifted in the mid-Eocene (Raven and Axelrod 1972). Furthermore, the barychelid found on Samoa occurred on the fringe of the sea, and was probably one of the few exceptions that proves the rule (Marples 1951).

The distribution of the Hexathelidae.—Of the three subfamilies, the monotypic subfamily Plesiothelinae is endemic to Tasmania. The Macrothelinae consist of *Macrothele*, which occurs throughout Laurasia and in Central Africa, and the Oriental region; *Porrhothele* which is endemic to New Zealand and is the sister group of *Macrothele*; and *Atrax*, which occurs throughout east coastal Australia from Tasmania northwards (Hickman 1964) to 24° North. The affinities of all species described by Rainbow (1920) suggest that the Papua locality was an error and thus the records of *Atrax* from Papua, and probably also those from the Solomon Islands (Rainbow 1913) and Cloncurry (Rainbow and Pulleine 1918) should be disregarded. The Hexathelinae include *Hexathelus*, which is endemic to New Zealand; its sister group, *Terania* is known only from southern Australia including Tasmania; *Bymainiella*, which occurs in south central coastal Australia; *Parembolides*, which is known from New South Wales and southern Queensland, Australia; and *Scotinoecus*, endemic to South America.

A biogeographical hypothesis.—Platnick and Nelson (1978) have provided several axioms for the testing of biogeographical hypotheses. However, the complexity of

possible events in historical biogeography fills the reconstruction of these events with secondary, non-testable hypotheses involving dispersal of organisms into areas already occupied by other members of the monophyletic taxon.

The ancestor of the Hexathelidae arose in East Antarctica in the early Jurassic, when Gondwanaland was still entire. This spider had dense labial and maxillary cuspules and six spinnerets, and the male had no tibial megaspines. Before Africa rifted northward in the mid-Jurassic to mid-Cretaceous (Vevers et al. 1971), this group radiated into Africa, India and throughout Antarctica.

Plesiothele arose soon after, near Tasmania, and probably had several related species. From the present localized distribution of this genus, it appears that it had low powers of vagility and its distribution was severely effected by the extent of Pleistocene glaciation in Tasmania.

In the ancestral sister group of *Plesiothele*, the anterior lateral spinnerets were beginning to reduce, but in other features it differed little from the ancestor of the Hexathelidae. From this ancestor arose two groups. One was a *Macrothele*-like ancestral spider group which had four spinnerets but no male tibial megaspine, which arose in East Antarctica and dispersed westward toward New Zealand and Australia. This is indicated by the contemporary widespread presence of *Macrothele* in Laurasia, Africa and India (Pocock 1903), and *Atrax* and *Porrhothele* in Australia and New Zealand. In fact, *Macrothele* or a close relative probably reached Australia and New Zealand just prior to the northward rafting of New Zealand in the late Cretaceous (Griffiths 1971). This would require that the Macrothelinae have superior dispersal mechanisms and adaptability than the Hexathelinae. This would account for the wide distribution of *Atrax* in Australia. One of the striking features of *Atrax* associated with its widespread distribution is the small morphological distance between its species. The greater dispersal ability hypothesised for *Atrax* is supported by the fact that there is usually considerable local differentiation in mygalomorphs which have poor dispersal ability (Forster, in Forster and Wilton 1968).

Although *Macrothele* is a widespread genus in Laurasia, such primitive cosmopolitanism does not conflict with the overall hypothesis (Platnick and Nelson 1978). However, the phylogeny of the Macrothelinae requires that *Porrhothele* and *Macrothele* are monophyletic and the biogeographic hypothesis requires that *Atrax* and *Porrhothele* were of most recent ancestry.

The sister group of the ancestor of *Macrothele*, *Porrhothele* and *Atrax*, to which I shall refer as plexathele, strongly resembled *Hexathele* except that the first leg of the male lacked any metatarsal excavation. Plexathele arose in East Antarctica near the Adelaide Geosyncline and was quickly divided into two groups. The vicariance event associated with this was probably the separation of East and West Antarctica by a marginal basin in the late Cretaceous (Craddock 1975).

In the male ancestor of *Hexathele* and *Terania*, a metatarsal excavation appeared. This ancestor was confined to the south eastern edge of Australia and New Zealand, and probably arose just before New Zealand rifted from the Antarctic continent in the late Cretaceous because, in the sister genus of *Hexathele*, the male *Terania* had lost one of the two tibial megaspines, which could not have occurred while New Zealand was still connected to Antarctica.

To the west of Tasmania arose the *Bymainiella*-like ancestral male, which retained at most two tibial megaspines, but that had a broad labium. The range of this group was from southern Queensland southwards, west of Tasmania (because no members of this clade are known from Tasmania or Victoria), through South Australia across Antarctica

into South America. This range was latter fragmented by a barrier (?aridity), thus giving rise to *Bymainiella* in the north, and the ancestor of *Paraembolides* and *Scotinoecus* in the south. The reduction of the anterior lateral spinnerets which diagnoses *Scotinoecus*, occurred subsequent to the rifting of Australia from Antarctica, which was the vicariance event that separated *Paraembolides* and *Scotinoecus*. *Paraembolides* was driven northward by the contraction of mesophytic beech forests in South Australia (Burbidge 1960). Eventually, *Paraembolides* invaded northern New South Wales and Queensland, thus accounting for its close allopatry with *Bymainiella* in these areas.

When a biogeographical hypothesis is constructed a sequence of geological events is proposed to explain the distributions. Because of the lack of specific agreement among geologists of times for the separation of the continents from each other (see Rich 1975) it is difficult to test the biogeographic hypothesis given. However, the separation sequence of the continents which is generally accepted for the theory of sea-floor spreading has been followed here. For Gondwanaland, that is: Africa - India - New Zealand - Australia - South America - all from Antarctica.

It is this sequence of events which prompts the question: Why are there no plesiomorphic hexatheline ancestors in South America, as there are in Australia? At this point, *Mediothele* Raven and Platnick 1978 appears to fill the requirements, but until further phylogenetic analysis indicates otherwise, the position of this genus must remain uncertain.

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